

The two physiological identities of the Common Hamster (*Cricetus cricetus* L.) – a race against the time of year

Die zwei physiologischen Identitäten des Feldhamsters (*Cricetus cricetus*) – ein Wettlauf gegen das Jahr

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Kurzfassung: In Anpassung an die Jahreszeiten zeigt der Europäische Feldhamster ausgeprägte saisonale Veränderungen in seiner Physiologie und im Verhalten. So wechseln sich Reproduktionszeit mit Winterschlaf und Zunahme mit Abnahme des Körpergewichtes im Jahresverlauf ab; Aktivitätsmuster und Melatoninproduktion variieren ebenfalls über das Jahr. Diese saisonalen Veränderungen haben eine starke endogene Komponente. Eine Besonderheit beim Feldhamster ist, dass das ausschließlich nachts produzierte Hormon Melatonin in der Zeit um den längsten Tag (kürzeste Nacht) nicht produziert wird (VIVIEN-ROELS et al. 1992). In unserer Studie suchten wir nach möglichen Korrelationen zwischen den oben beschriebenen Parametern. Eine vorläufige Auswertung der Daten zeigt eine Korrelation zwischen der auffälligen Phase fehlender Melatonin-Produktion, einer Phase im Aktivitätsmuster, welche sich durch einen äußerst exakten 24 h Rhythmus auszeichnet, und einer von SABOUREAU et al. (1999) postulierten sensitiven Phase für Kurztag-Information zwischen dem 15. Mai und dem 15. Juli. Vier Wochen später begann die Gonadenregression. Dieses Kurztag-Signal ist für die Tiere von höchster Bedeutung, denn zum einen zeigt es den bevorstehenden Winter an und ermöglicht dem Feldhamster eine rechtzeitige Vorbereitung des Winterschlafs und zum anderen stellt es vermutlich die endogene Jahresuhr, welche für das korrekte „timing“ der Gonaden-Regeneration im Frühjahr und der sensitiven Phase im nächsten Sommer verantwortlich ist. In dieser sensitiven Phase vom 15. Mai bis 15. Juli könnte jede Störung der Tiere durch künstliches Licht oder Einfangen und Umsiedeln dazu führen, dass die Tiere dieses lebensnotwendige Signal verpassen.

The natural habitat of the Common Hamster is characterized by dramatic changes in day length (photoperiod) resulting in pronounced modifications in climate and vegetation over the year. In adaptation to these important environmental conditions the Common Hamster exhibits pronounced seasonal variations in its physiology and behavior.

For the Common Hamster, the year starts in a hibernating state deep under the earth without any information about the time of day and the time of year. Nevertheless, at a certain time in early spring the reproductive system, which was degenerated during wintertime, shows a spontaneous regeneration. When it is completely developed, the Common Hamsters leave their burrows and search for a mating partner. It is remarkable that all these solitarily living animals leave their burrows almost simultaneously around the beginning of March without having any information about the time of year, suggesting that they have some sort of an internal clock controlling this process. Spring and summer time are characterized by reproduction and breeding. However, when the days become shorter in late summer the gonads start to regress again and the animals hoard food for the coming winter. In autumn the animals vanish into their burrows in order to hibernate again until the following spring (PÉVET et al. 1989).

The body weight follows an annual cycle, too. In spring and summer the body weight increases strongly, whereas it decreases slightly in autumn and winter. This is not a reaction to the poor availability of food in winter. Instead, it has been shown that there is a regulating mechanism, which undergoes circannual variations (CANGUILHEM & MARX 1973). The decrease of body weight in the second half of the year serves the purpose to save energy during hibernation, because a smaller body has a smaller surface and thus a minor heat loss.

In addition to the seasonal cycles of the reproductive state and body weight, the temporal organization of the activity changes in a seasonal manner (WOLLNIK, BRETT & REINKE 1991). Only during a few months in the middle of summer the Common Hamster is mainly nocturnal and shows high amounts of activity per 24 hours. In autumn the rhythmicity vanishes slowly, the activity level decreases, and the animals become completely arrhythmic during the winter.

According to the present state of knowledge, the hormone melatonin is strongly involved in seasonal changes of behavior and physiology (PÉVET 2000; REITER 1988). The hormone melatonin is produced by the pineal gland only at night and released into the blood circuit. Therefore, every cell of the body receives information about at least two times a day, namely day (if there is no melatonin) and night (if there is a certain level of melatonin). Depending on the night length the duration and amplitude of the melatonin signal varies. As a result melatonin also indicates the time of year. In the long winter nights there is a long, pronounced peak of melatonin release, which gets shorter and weaker when days become longer. It is unique for the Common Hamster that around the longest day (shortest night) on June 21st, there is no nightly melatonin elevation at all, neither in the pineal gland nor in the blood (VIVIEN-ROELS et al. 1992; 1998; 1997).

SABOUREAU et al. (1999) have demonstrated that Common Hamsters have a sensitive phase for short days, which starts approximately on May 15th and ends around July 15th. Prior to that phase the animals are not able to interpret the current photoperiod. If the animals notice during that sensitive time that the day length becomes shorter, they react with a regression of their gonads and prepare for hibernation. It takes approximately 4 weeks from the perception of the short-day signal until the first visible reduction of the gonads takes place. The timing of this sensitive phase is most likely endogenous. The end is determined by the day when the animals recognize a reduced day length, which happens around July 15th under natural conditions. In Strasbourg, where the investigation took place, day length shortens only about 1 min/d during the time between June 21st and July 15th. That means that first the animals are extremely sensitive for the short-day signal and that second it is very important for them to receive the signal on time. Otherwise they may be late with their hibernation cycle, which could mean they do not survive.

In summary, it can be said that Common Hamsters show pronounced changes in their physiology and behavior, which have a strong endogenous component. The aim of the present investigation was to look for a possible correlation between the

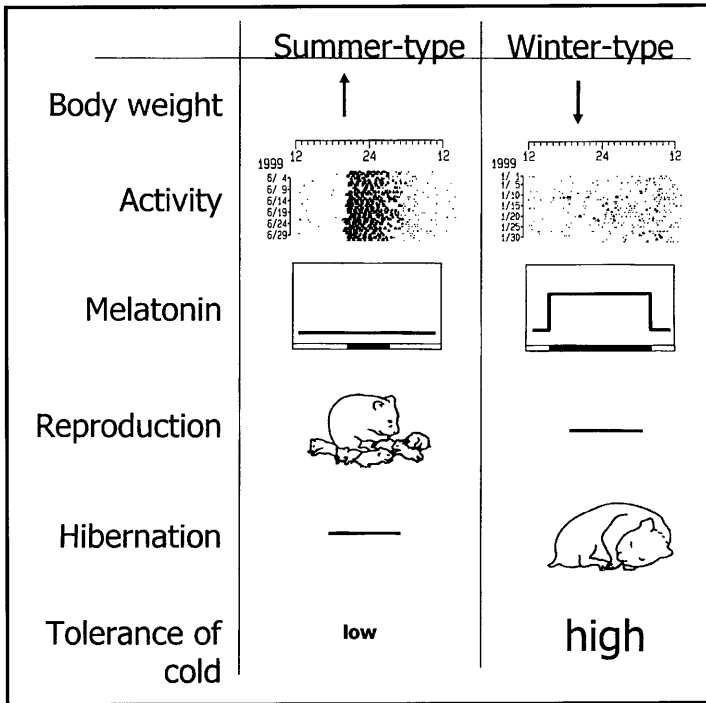


Figure 1: The two physiological identities of the Common Hamster
Abbildung 1: Die zwei physiologischen Identitäten des Feldhamsters

parameters discussed above. For that reason, the wheel running activity of 8 Common Hamsters (3 male, 5 female) was registered over one year under natural lighting conditions, but constant temperature (20 ± 1 °C) and humidity ($55 \pm 5\%$). Body weight and reproductive status were controlled every three weeks. Additionally, the animals' urine was collected at every „full“ photoperiod (e.g. 10 h of light, 11 h of light, 12 h of light etc.) in 2 h intervals over 24 h in order to determine it's content of 6-sulfatoxymelatonin (aMT6s) in each fraction. aMT6s is the main catabolism product of melatonin which is excreted with the urine.

A preliminary analysis of the data revealed the following results: As has been demonstrated for melatonin levels in the blood or in the pineal gland (VIVIEN-ROELS et al. 1992; 1997; 1998), the present study revealed a distinct day-night difference in aMT6s excretion during fall, winter and spring. In contrast, no nightly elevation of aMT6s was observed in the middle of summer. The phase of low or absent aMT6s excretion starts somewhere in the middle of May with an obvious inter-individual variability between animals. In contrast, the phase ends more or less consistently in the middle of July. The activity patterns of all animals showed one striking characteristic: There was a phase in the middle of summer, when the

pattern had a very precise 24 h rhythm, i.e., the animals began to run at the same time each day in the early evening, no matter if it was already dark or still daylight, since sunset shifted from day to day. Similar to the phase of absent aMT6s, the striking phase in the activity pattern started also somewhere between April and the beginning of June, but it ended quite simultaneously in all animals in the middle of July. SABOUREAU et al. (1999) found that the sensitive phase for short days ends as well in the middle of July with the reception of the short day signal. The start of the gonad regression occurs 4 weeks later. The present data also show that approximately 4 weeks after the reappearance of the nightly melatonin signal and the disappearance of the precise 24 h activity pattern described above, the gonads of the animals started to regress. Concurrently the body weight decreased. Therefore, it seems that the peculiar phase in the middle of summer, which is characterized by an absent melatonin excretion on one hand and a rather precise activity pattern on the other hand, correlates with the sensitive phase for short day information which has been postulated by SABOUREAU et al. (1999).

Since the daily profile of melatonin production and the activity pattern are both output parameters of the endogenous circadian clock, the present data indicate that something is altered in the circadian clock during the sensitive phase in the middle of summer. This change in the circadian system may cause the increased sensitivity for short days. Furthermore, our data raise the hypothesis that either the reappearance of a daily melatonin peak or the change in the activity pattern may provide the necessary „winter signal“. Alternatively, it may be possible that they simply coincided with an undiscovered hormonal or neuronal signal. Further investigations are necessary to prove these hypotheses.

Whatever mechanism may be responsible for the increased short-day sensitivity, it seems to be connected with the circadian clock located in the suprachiasmatic nuclei (SCN) in the hypothalamus (KLEIN, MOORE & REPPERT 1991). Changes in daylength are perceived by the circadian system within the SCN and are most likely transferred from the SCN to the circannual clock, the location of which is still unknown. At the present time, the nature of this signal (humoral or neural) is still a mystery. Nevertheless, there is no doubt, that the signal is very important for the resetting of the circannual clock, which times the regeneration of the gonads in spring and the new sensitive phase in the summer of the following year.

Since it can not be excluded that the daily melatonin or activity patterns are responsible for the necessary sensitivity for short days in summer, it is advisable to not disturb the animals' sensitivity by artificial light or by capture. The influence of artificial light during the night should be avoided, because it may interfere with the release of melatonin from the pineal. Capture and resettlement of the animal may lead to stress and thus to higher activity at the wrong time. This may affect the activity pattern for several days and may disturb the sensitivity for short days. As a consequence, the Common Hamster may miss the important „winter- and reset-signal“, and its annual rhythm of physiology may be disturbed for an entire year.

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